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The life-history of *Surendra florimel* DOHERTY 1889 (Lepidoptera: Lycaenidae) in West Malaysia

by

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Abstract: The early stages of the Oriental hairstreak butterfly *Surendra florimel* DOHERTY 1889 are described for the first time. Larvae feed on young foliage of certain Mimosaceae lianas. Second and third instars also visit extrafloral nectaries. From the second to the fifth instar the larvae possess a dorsal nectary organ (DNO) and paired tentacle organs (TOs). Most caterpillars are tended by ants from at least 5 ant genera. Both larvae and pupae almost constantly produce substrate-borne vibrations, but an airborne component is likewise present. A parasitized larva was attractive to ants beyond the emergence of the parasitoid larva and retained its vibratory abilities for 7 days. The pupae lack a functional DNO, but at the locations of the larval TOs there is a peculiar paired organ (homologous to the TOs?) of unknown function. Further epidermal organs of larvae and pupae are described.

Der Lebenszyklus von *Surendra florimel* DOHERTY 1889 (Lepidoptera: Lycaenidae) in Westmalaysia

Zusammenfassung: Die Präimaginalstadien von *Surendra florimel* DOHERTY 1889 (Lycaenidae: Lycaeninae: Theclini: Arhopaliti) werden erstmalig beschrieben. Wirtspflanze in Westmalaysia ist eine lianenartige Mimosacee. Die Eiablage erfolgt einzeln an sehr jungen Trieben, die Präsenz von Ameisen ist dabei nicht entscheidend. Die Raupen fressen ausschließlich junge, kaum entfaltete Blätter. Im 2. und 3. Stadium besuchen sie zudem intensiv extraflorale Nektarien. Vom 2. bis 5. Stadium besitzen die fakultativ myrmekophilen Larven ein dorsales Nektarorgan und paarige Tentakelorgane. Die Mehrzahl der Raupen wird von Ameisen aus mindestens 5 Gattungen besucht. Raupen und Puppen produzieren zweikomponentige Substratvibrationen: eine permanente „raschelnde" Grundvibration und bei Störung pulsartige, höherfrequente „krächzende" Signale (letztere enthalten auch luftgetragene Anteile). Eine parasitierte Raupe blieb noch über das Auskriechen der Parasitoiden-

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larve hinaus für Ameisen attraktiv und konnte noch 7 Tage lang Vibrationen hervorbringen. Die Puppen haben kein funktionsfähiges Nektarorgan, besitzen aber in gleicher Position wie die larvalen Tentakelorgane ein Paar lateraler Organe (homolog zu den Tentakeln?) unbekannter Funktion. Weitere Epidermalorgane der Raupen und Puppen werden beschrieben und mit vorhandenen Angaben zu den Subtriben Arhopaliti und Thecliti verglichen.

Introduction

Among the Oriental lycaenid butterflies the by far greatest species diversity (approx. 240 described species: BRIDGES 1988) is found in the hairstreak subtribe Arhopaliti BINGHAM 1907. From the island of Borneo, for example, SEKI et al. (1991) reported 379 species of Lycaenidae, 97 (= 25.6 %) of which belong to the Arhopaliti. *Arhopala* BOISDUVAL 1832 alone accounts for 91 species (= 24 %) there. Available information on the ecology and life-history of Arhopaliti hairstreaks, however, is extremely scanty. At present, early stages and/or hostplants are known from less than 30 species (FIEDLER 1991 a). This poor figure is, among the Lycaenidae, only rivalled by the subfamily Poritiinae and is a major obstacle to a comprehensive analysis of the evolution and maintenance of the amazing species diversity of the Arhopaliti in the Oriental rainforests.

Surendra MOORE [1879] is a small genus of this subtribe with 4–5 currently recognized species that range from India and Sri Lanka across Sundaland to Sulawesi and the Philippines. The early stages of two species, *S. vivarna* (HORSFIELD [1829]) and *S. quercetorum* (MOORE [1858]) (this latter taxon is sometimes considered to be a subspecies of the former), have been described so far (BELL 1915, MASCHWITZ et al. 1985). Between October and December 1991, I had the opportunity to study the early instars of a third species, *S. florimel* DOHERTY 1889 (Fig. 1), in West Malaysia. *S. florimel* has a typical Sundaland distribution from southern Myanmar (formerly Burma) to Sumatra, Borneo and Java. The purpose of the present paper is a) to make available these observations and b) to compare the results with morphological and ecological data on other Arhopaliti species.

Study area, habitat and hostplant

All observations took place in the immediate vicinity of the Ulu Gombak Field Studies Centre of the Universiti Malaya, ca. 20 km north of the Malaysian capital Kuala Lumpur. This area (altitude 200–400 m)

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is situated at the foothills of the Genting highlands and is mainly covered with advanced secondary forest of the lowland dipterocarp type.

The only hostplant of *S. florimel* observed in the study area was a thorny creeping leguminous vine of the family Mimosaceae. Although hundreds of saplings and young growth of a number of further Mimosaceae, Caesalpiniaceae and Fabaceae species were regularly checked for the presence of lycaenid immatures over a 7-weeks period, none of these yielded any eggs or larvae of *S. florimel*. Furthermore the caterpillars refused to feed on several Mimosaceae species that were tested as alternative food. Thus *S. florimel* has a restricted range of acceptable hostplants and might even be (locally) monophagous. A thorough determination of the hostplant is yet impossible, since neither flowers nor seed pods were produced during the observation period.

Saplings of the hostplant (0.3–1.0 m height) were locally common in the shaded understory of dense forest, while larger plants (up to 5 m) were found at the edges of streets, small forest clearings or jungle gaps. The hostplant was practically absent from larger (and thus very sunny) forest clearings. Eggs and larvae of *S. florimel* were found regularly in the understory, even in a truly swampy forest patch, as well as at the verges of roads and logging paths, but never beyond the shade of tall trees.

Oviposition

On 28 November 1991, 15.00 local time, a female was observed ovipositing on a very young, tender leaf of a creeping shoot, approx. 1 m above ground. The female first examined the hostplant while fluttering along the shoot, then settled down, probed the substrate with the abdominal tip, and then placed a single egg on the developing leaf. The whole procedure took less than 1 min, then she left the plant and flew away. The shoot carried an active extrafloral nectary (EFN hereafter), but no ants were actually present. A neighbouring shoot of the same plant occupied by a second instar larva was rejected for oviposition. This caterpillar was not attended by ants at the time the female laid her egg, but 20 min later it was visited by a single ant (*Technomyrmex* sp.).

Despite intensive search only 2 further eggs and one empty egg-shell could be located during the whole observation period, all 3 again on very young and tender leaves that had not yet been unfolded at the time of oviposition. One of these eggs was collected on 2 November,

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and the larva hatched on 5 November. No ants were seen on the twigs carrying the eggs.

These observations suggest that *S. florimel* females select very young leaves on growing shoots of their hostplants with conspicuous EFNs. They predilect plants growing in shady conditions and always oviposit singly, apparently avoiding shoots that are already colonized by caterpillars. Ants are clearly not necessary as (additional) oviposition cue.

The larva: General morphology, behaviour and ecology

FIRST INSTAR: I found only one L_1 in the field (5 December). This caterpillar sat on a young, not unfolded leaf of a shoot, ca. 1 m above ground with no ants in attendance. In captivity it fed only on the youngest leaf tissues. Another first instar that hatched from the egg collected on 2 November, lived in captivity for only 5 d. It fed reluctantly on very young foliage, gnawing small holes in the leaflets. Only fresh food was accepted, and the larva refused feeding within a few hours when the food started to wilt. First instars of *S. florimel* obviously are specialized feeders of the youngest and most tender parts of the foliage. The L_1 is uniformly light-green and grows to ca. 3 mm in length.

SECOND INSTAR: Second instars are likewise uniformly green and reach a length of 5 mm. In contrast to the more or less cylindrical first instars, the L_2 larvae exhibit the typical flattened, "onisciform" shape. They also possess a dorsal nectary organ (DNO) on the seventh abdominal segment (A7) and a pair of tentacle organs (TOs) on A8. Second instars were mostly visited by ants, although the associations tended to be unstable. One L_2 was found without any attendant ants, 2 L_2 were associated with a small brown *Crematogaster* sp. (Myrmicinae), one with a *Tapinoma* sp. (this ant repeatedly left the caterpillar), and one with *Technomyrmex* cf. *albipes* (both Dolichoderinae). In the latter case, the caterpillar was not tended when observed first, but was tended 20 min later. Although second instars were antennated very often, I could not observe secretions from the DNO with certainty, nor were the TOs everted. Possibly these myrmecophilous organs are not fully developed and functional at this early stage.

One behavioural characteristic of the second instars was highly conspicuous: all second instars were found sitting on the leaf stalks with their heads in contact to the large EFNs of the hostplant (Fig. 5). The larvae remained at these organs even in captivity for hours. Although

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I could not demonstrate this with certainty, the larvae appeared to harvest EFN secretions. One L_2 moulted in this position.

THIRD INSTAR: From the third instar onwards, the larvae develop a characteristic colour pattern: a lateral series of 7–8 oblique whitish stripes between the second thoracic (T2) and sixth abdominal segment (A6). Each of these stripes is ventrally marked with a dark green border. In addition, the dorsal midline is marked by a dark green line from T2 to the rear end, whereas the lateral margin carries a distinct light-greenish edging. The ground colour remains a light green that closely matches the colour of young hostplant foliage. Altogether, the colour markings of the third to fifth instars result in a mimetic pattern that makes the caterpillars difficult to detect among the young pinnate leaves of its mimosaceous hostplant.

During daytime, third instars were found sitting on the upper part of the stalks of young shoots or at EFNs, a few centimeters away from the young leaves on which they feed. In captivity most feeding activity was observed at night, suggesting that the caterpillars are largely nocturnal. They grew to ca. 9 mm in length. In captivity the third instar lasted 5–8 d.

Third instars are mostly ant-tended. Only 2 out of 11 L_3 were not visited by ants at the time of collecting, and one of these was found on a plant within the territory of the aggressive and dominant weaver ant *Oecophylla smaragdina*. This could have prevented smaller ant species from associating with the caterpillar. The remaining 9 L_3 caterpillars were visited by 1–3 worker ants each belonging to 5 genera in 3 ant subfamilies (Table 1).

Table 1: Numbers of *Surendra florimel* larvae observed in the field with or without ants in attendance. I–V are the instar numbers. *Crematogaster* sp. 1 is a small brown species, *Crematogaster* sp. 2 a larger black one (near *C. difformis*).

Tending ants	I	II	III	IV	V
Myrmicinae:					
Rhoptromyrmex wroughtonii			2		
Crematogaster sp. 1		2	3	1	
Crematogaster sp. 2			1	1	
Dolichoderinae:					
Tapinoma sp.		1	1		
Technomyrmex cf. *albipes*		1		1	
Formicinae:					
Paratrechina sp.			1		
no ants	1	1	2	1	1

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FOURTH INSTAR: These are very similar to L_3 larvae in colour pattern and behaviour (Fig. 6). Again most feeding activity occurred at night, and 3 out of 4 L_4 collected in the field were ant-tended (Table 1). The fourth instar took 5—10 d in captivity, the larvae reaching ca. 14 mm in length.

FIFTH (FINAL) INSTAR: The L_5 larvae retain the mimetic stripe pattern (Fig. 2), but their shape somewhat changes. In a lateral view they are now smoothly humped instead of largely flat and thus closely resemble a developing pinnate leaf (mimesis, Fig. 4). At least in captivity, L_5 larvae fed day and night, but they still strongly preferred young tender leaves. Mature foliage was rejected. Only 1 fifth instar was observed in the field resting on the hostplant stem in the late afternoon without attendant ants. This caterpillar pupated after 8 d. In captivity, the final instar lasted 10—14 d (maximum length 20—22 mm).

Two days prior to pupation the larvae stop feeding, and their green ground colour turns into purplish brown (Fig. 3). Then they settle down on a silk pad and moult into a girdled pupa after a prepupal phase of 1—2 d.

The larva: Myrmecophily and substrate-borne vibrations

Second to fifth instar caterpillars of *S. florimel* are usually tended by ants, the larval attractiveness steadily increasing with larval development. While second instars are only from time to time antennated by their tending ants, mature larvae basically maintain permanent ant-associations. Nevertheless, *S. florimel* has no obligatory or specific symbiosis with ants, as evidenced by the fact that ants of various genera and subfamilies are attracted (Tab. 1). A few larvae, including 2 late instars, were also found without ants in the field. Accordingly, *S. florimel* can be assigned to the group of steadily, but facultatively myrmecophilous lycaenids following the classification of FIEDLER (1991 b).

Besides the ant-associations recorded in nature (Table 1), I also introduced worker ants of another *Crematogaster* species and of the formicine *Polyrhachis bellicosa* (Fig. 4) to fourth and fifth instars. Both these ant species intensively tended the caterpillars. In captivity, *Technomyrmex* (Fig. 6) and all 3 *Crematogaster* species were associated with the caterpillars day and night. In contrast, one worker of *Paratrechina* sp. was mostly inactive and hidden during daytime, but intensively visited a third instar larva while feeding at night. *Polyrhachis bellicosa* showed the reverse behaviour, tending the larvae during day-

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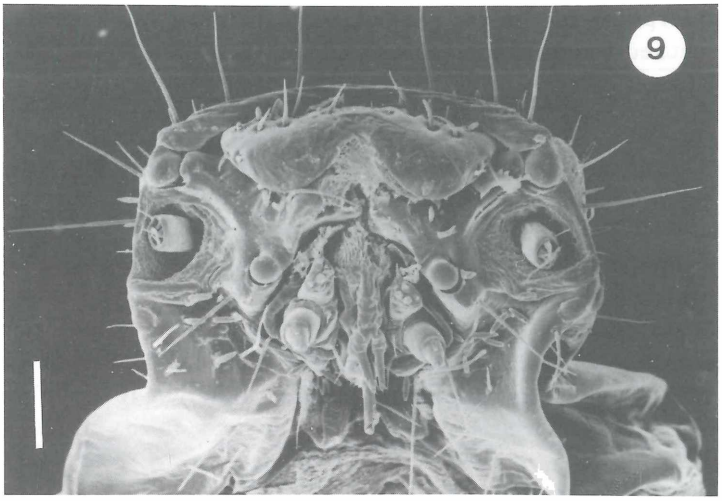

Fig. 9: Fifth instar larva, head (ventral view). Scale: 150 μm (courtesy D. KOVAC).

time, but resting away from these at night. Such a diurnal activity pattern of certain trophobiotic ant species might explain the lack of attendant ants at some caterpillars. Possibly, these particular larvae received ant-attendance only during night-time, when the caterpillars normally feed, but were left alone while resting.

When tending the larvae, the ants intensively antennated the whole body and often nibbled with their mandibles at the cuticle. The whole caterpillar was attractive, suggesting that other epidermal glands besides the DNO are also important in the ant-symbiosis of *S. florimel*. After intensive antennation, the ants often groomed their antennae (and sometimes also the tarsi) by pulling them through their mandibles. This behaviour was especially pronounced in the case of *Polyrhachis bellicosa* and might represent a method of harvesting the secretions of the pore cupola organs (PCOs) and other hairs (see below). From time to time, the region of the DNO was visited, and L_3–L_5 caterpillars often responded to this tactile stimulation with the secretion of nectar-like droplets. These were immediately licked up by the ants. While most ants took such droplets with their mandibles, *Polyrhachis bellicosa* again provided an exception: these large ants used their maxillary palpi to collect the secretions (Fig. 4). When a caterpillar-ant association had been well established (e. g. after ants and caterpillars had been kept together in captivity for some hours), the frequency of DNO secretion-acts decreased and the ants often sat motionless on the back

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of the caterpillar for longer periods. Any disturbance, however, immediately caused the ants to resume agile antennation of the caterpillar.

The caterpillars often everted the TOs, especially during the first hours when they were caged with ants, or after being disturbed (e. g. manipulating the caterpillars with forceps). The ants readily responded with a kind of alert behaviour, but only if they had close contact with the everted TOs. *Technomyrmex, Tapinoma* and all 3 *Crematogaster* species showed typical "excited runs" (FIEDLER & MASCHWITZ 1988): these ants suddenly dashed over and around the caterpillar for 3–10 s and then returned. Mostly these excited runs started with a rapid jerking movement directed towards one TO. The small brown *Crematogaster* sp. 1 exhibited an additional peculiar reaction towards TO eversions: the ants performed a trembling up-and-down movement with their gaster. I have observed this behaviour as a reaction towards lycaenid caterpillar TOs with the same ant species also at larvae of *Prosotas dubiosa* (SEMPER [1879]) and *Jamides* sp. (FIEDLER, unpubl.). Occasionally "excited runs" as well as "gaster-trembling" occurred without foregoing TO eversion.

The remainig ant species tested (*Rhoptromyrmex wroughtonii, Polyrhachis bellicosa, Paratrechina* sp.) did not exhibit true "excited runs", but they also performed characteristic jerks towards everted TOs. Thus, caterpillars of *S. florimel* are able to alert a broad taxonomic variety of tending ants with the help of their TOs.

At present, a precise evaluation of the costs and benefits of myrmecophily in the case of *S. florimel* is impossible. Nevertheless, some observations on survival of ants that received no other food besides larval secretions indicate that ants may derive substantial nutritive benefits. For example, 3 *Technomyrmex* workers survived 10 d, one *Crematogaster* worker 16 d, 3 *Rhoptromyrmex* ants 7 d and one *Paratrechina* ant 6 d, all caged with a single caterpillar each. The ants were still alive at the end of all these trials, while ants caged with pupae or myrmecoxenous lycaenid larvae often die within 1–2 d (FIEDLER & SAAM, unpubl.).

Like numerous other lycaenid larvae (DEVRIES 1991 b, SCHURIAN & FIEDLER 1991), the caterpillars of *S. florimel* are capable of producing substrate-borne vibrations from the third instar on. Using a Bauer & Häselbarth lightweight stethoscope, these vibrations could easily be perceived; they are not audible to the unaided human ear because there are usually no air-borne components involved: DEVRIES (1991 b), FIED-

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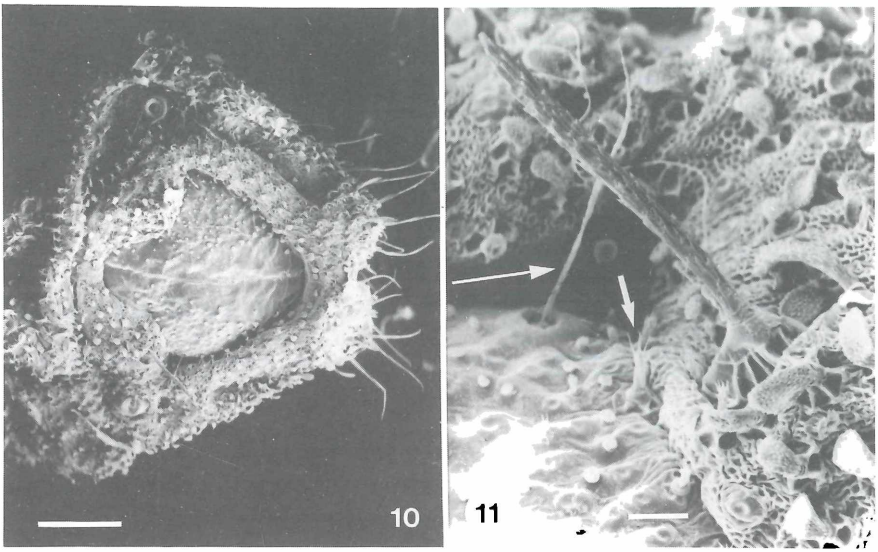

Figs. 10–11: Prothorax of mature larva, dorsal view. **Fig. 10:** Prothoracic shield; note smooth cuticle. Scale: 150 μm. **Fig. 11:** Latero-posterior edge of prothoracic shield with straight single sensillum. Thick arrow: dendritic seta; thin arrow: filiform seta. Scale: 100 μm (courtesy D. KOVAC).

LER & KIRCHNER (unpubl.). As in many other Lycaenidae, vibratory signals of *S. florimel* consist of two different components. One is a "rustling" or crackling vibration of low amplitude. This vibratory component is produced almost constantly, even when the caterpillars remain undisturbed on the stethoscope membrane. The second component are short "cackling" or chirping pulses of distinctly higher carrier frequency and amplitude. These pulses are mainly produced when the caterpillars are molested (e. g. with forceps), the number of calls and their amplitude increasing with the severity of disturbance. These pulse components were audible to the human ear at a distance of 5—10 cm, when the caterpillars were placed on the stethoscope membrane, but without using the ear-connecting tubes.

The larva: Epidermal organs

The cuticle of *S. florimel* larvae shows the crinkly honeycomb structure typical for many lycaenid caterpillars. The well developed prothoracic shield (Fig. 10) and anal plate, however, have a smooth cuticle.

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Two groups of epidermal organs are especially important in lycaenid larvae: the myrmecophilous glands (DNO and TOs) and the various types of secondary setae (mostly these are sensory, but also secretory as in the case of the pore cupola organs). The following types of setae have been found on mature larvae of *S. florimel* (numbers refer to mature larvae; the number and density of secondary setae increases dramatically from L_2–L_5):

1) Long straight bristles (150–500 μm); these only occur on the ventral side and along the lateral margin of the larva (Fig. 10), but in large numbers.

2) Single long hairs (ca. 330 μm) with a dentate hair shaft; one such hair occurs on either side of the dorsum on an epidermal bulge of T1 (directed anteriorly; Fig. 11) and on A4–A6 (directed posteriorly).

3) Filiform setae (270 μm) with a very slender, smooth hair shaft; one filiform seta each is inserted near the latero-posterior margin of the prothoracic shield (Fig. 11).

4) Dendritic setae (20–30 μm); small groups of these have been found at three different locations. At the posterior edge of the prothoracic shield there are ca. 5 dendritic hairs on each side (Fig. 11), around the first abdominal spiracle there is a large group of 15–20 dendritic setae on either side, and at both lateral edges of the DNO there are again small groups of ca. 5 hairs (Figs. 14 & 15).

5) Curved hairs (40–70 μm) with a flattened, club-like distal end and a rough, "spiny" surface (Fig. 12); such hairs are the most abundant setal type and occur in large numbers all over the dorsal surface of the caterpillar of *S. florimel*, practically replacing the straight hairs of many lycaenids as main hair type. At certain locations (e.g. near the DNO and TOs), there occur similar hairs that are not strongly curved (Figs. 14 & 15).

6) "Mushroom-like" setae (40–50 μm) with a flattened and broadened, disk-like distal end (diameter 30–40 μm; Fig. 13). The surface of these hairs shows a honeycombe-like structure, suggesting the presence of cavities or openings in the hair. Mushroom-like setae are particularly abundant around the DNO and TOs (Figs. 14–18).

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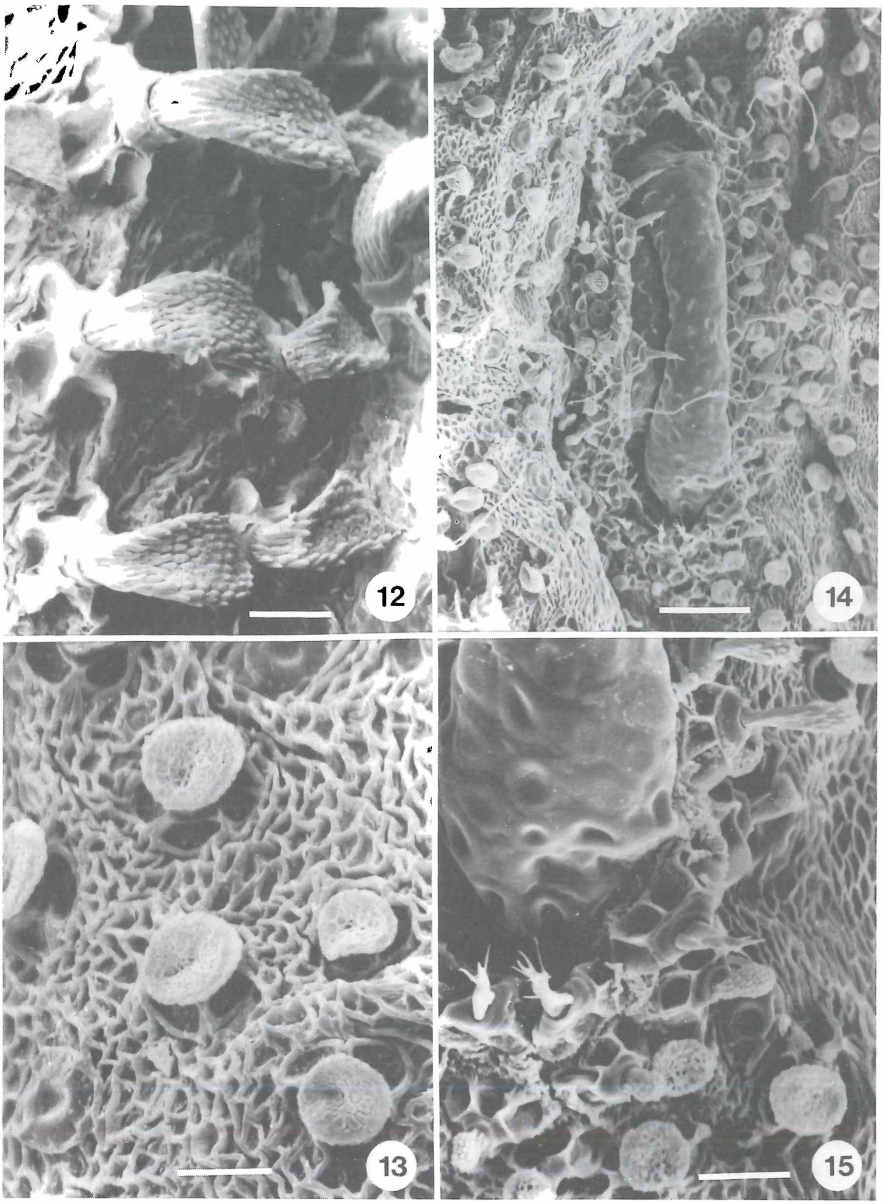

Figs. 12–15: Organs of mature caterpillar of *S. florimel*. **Fig. 12:** Flattened club-shaped setae. Scale: 30 μm. **Fig. 13:** Mushroom-like setae and pore cupola organ (PCO). Scale: 30 μm. **Fig. 14:** Dorsal nectary organ (DNO) with surrounding modified setae. Scale: 100 μm. **Fig. 15:** Lateral edge of DNO. Note small group of dendritic hairs and PCOs in the membraneous, eversible part of the DNO cuticle. Scale: 30 μm (courtesy D. KOVAC).

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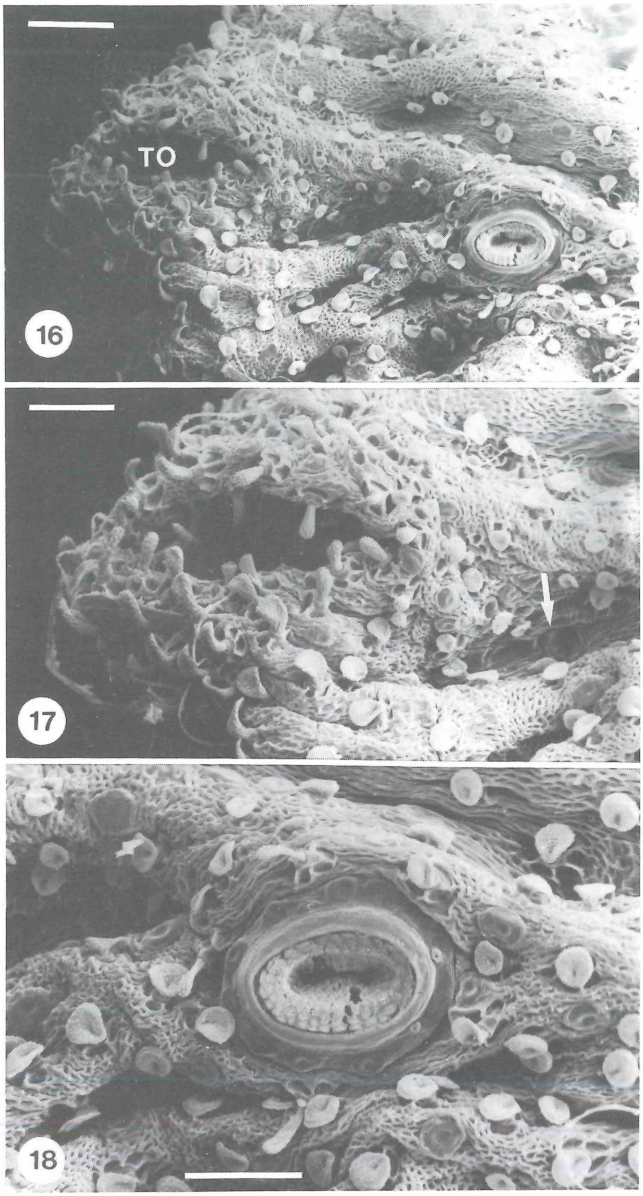

Figs. 16–18: Eighth abdominal segment of mature *S. florimel* caterpillar. **Fig. 16:** Overview with inverted tentacle organ (TO), spiracle and epidermal pores. Scale: 150 μm. **Fig. 17:** Inverted TO on elevated bulge. Arrow: epidermal pore. Scale: 100 μm. **Fig. 18:** Spiracle of A8, surrounded by PCOs and mushroom-like setae. Scale: 100 μm (courtesy D. KOVAC).

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7) Cone-like smooth setae (45 μm); 3–5 of such setae occur at each prothoracic spiracle.

8) Pore cupola organs (PCOs); these hairs (diameter 30 μm) lack a true shaft and are found scatteredly all over the larva. A very dense cluster of PCOs occurs within the membraneous cuticle surrounding the DNO opening (Fig. 15). Larger numbers of PCOs also occur around the spiracles (Fig. 18).

Further setae, including some apparent transitional types between curved and mushroom hairs, have also been seen, but their interpretation requires a detailed comparison across the larval instars based on larger material.

S. florimel larvae possess a DNO on A7 from L_2–L_5, which is functional at least from L_3 onwards. In the final instar larvae the DNO opening is ca. 450 μm broad and surrounded by many PCOs (Figs. 14 & 15). The TOs are situated in conspicuous elevated epidermal bulges at the lateral edges of A8 (Figs. 16 & 17). Both myrmecophilous organs are accompanied by specialized setae (mainly types 4–6). Club-shaped setae even occur on the inner wall of the elevated TO sheaths. The tip of the everted TOs also bears club-shaped setae.

Besides these two gland types there occur epidermal pores on most segments. Between the spiracles of A8 and the TOs, for example, there are 3 such pores on either side (Figs. 16–18). It remains to be examined whether or not these pores are connected with glandular tissues.

The pupa

The sturdy pupae are 9–12 mm long and fastened to the substrate with a girdle and a silk pad at the cremaster. In captivity, pupation occurred between hostplant material or filter paper spun together with some loose silk threads. The pupal ground colour is brown, with a reddish or purplish hint in the first days, but later turning into yellowish brown. The pupa is mottled with blackish dots all over (Fig. 7). Along the dorsal midline there is a continuous row of larger blackish dots from the head towards A6. Another row of prominent black dots is situated between the midline and the spiracles running from A2–A6. On A7, this row converges to two dark spots at either edge of the DNO scar. The prothoracic spiracle is also marked with black.

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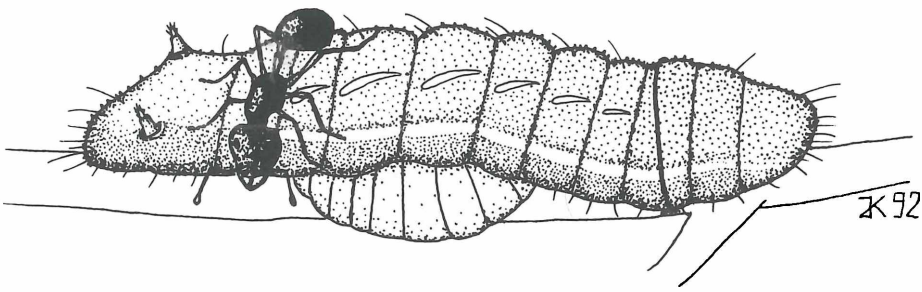

Fig. 19: Third instar caterpillar. A parasitoid larva has emerged ventrally, while the caterpillar is still tended by a worker ant (*Rhoptromyrmex wroughtonii*). Note the everted TOs. Drawing by J. KLEIN after a photograph by K. FIEDLER.

Two days days before eclosion, the eyes become pigmented and on the following day the whole pupa changes into dark blackish brown. Eclosion took place after 10–13 d in captivity (temperature 20–25 °C, ambient light conditions).

The pupal cuticle carries the usual network of elevated anastomozing ribs. PCOs or other hair-derived structures occur on the locations where such ribs converge. The following setal types were recognized:

1) PCOs (diameter 10–30 μm, Fig. 23) occur scatteredly all over the dorsal and lateral pupal cuticle (except the wing cases), but there are large clusters around the abdominal spiracles, especially on A5 and A6.

2) Trumpet-shaped hairs (length 30–40 μm, Fig. 24) likewise occur all over the pupa, but they are rare at the rear end and absent from the spiracle regions of A5–A7 as well as from the wing cases.

3) Dendritic setae (30–50 μm, Fig. 25) occur in a large group (ca. 20 on each side) around the spiracle of A6.

At the spiracles of A4 and A5 there are fewer (ca. 5) straight hairs that lack the characteristic thin branches of the true dendritic setae. At the cremaster there is a ventral field of hook-like bristles (Fig. 26) that help to attach the pupa to its silk pad.

A scar of the DNO is well discernible on A7 (Figs. 20 & 21), but there is no evidence of a glandular opening or other cuticular modifications. PCOs and trumpet jairs occur around this scar, but not with a higher density than elsewhere on the pupa.

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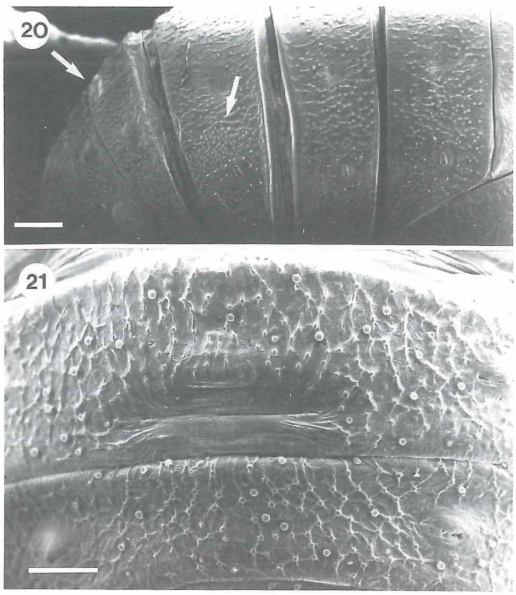

Figs. 20–27: Pupal epidermal organs

Fig. 20: Abdomen, lateral view. Arrows indicate spiracle of A6 with prominent cluster of PCOs and location of DNO scar on A7. Scale: 0.5 mm. **Fig. 21:** Scar of DNO on A7, surrounded by a few PCOs and trumpet setae. The non-functional spiracles on A7 and A8 are visible near the right margin. Scale: 250 μm.

The most remarkable of all pupal structures is found laterally on A8 (Figs. 20 & 22). It consists of a nearly hemispherical "dome" (diameter 350–400 μm) that is densely covered with minute (20 μm), stiff bristles. In the middle of each organ there is a small depression devoid of bristles, but a glandular opening is not discernible. Around the verges of the lateral organs there occur several PCOs, and at a distance of 100 μm there is a specialized cuticular field (diameter 150 μm) lacking the usual rib network.

The intersegmental areas of A4–5, A5–6 and A6–7 are modified and flexible (Fig. 20). There are cuticular warts and teeth on all three locations, but a fully developed stridulatory organ (with plate and file) was only seen between A5 and A6 (Fig. 27). Nevertheless, all three intersegmental areas may be involved in sound production.

The pupae of *S. florimel* produce the most complex vibratory signals I have thus far heard in roughly 25 lycaenid species. Like in the larvae there are two components: a nearly permanent rustling vibration with

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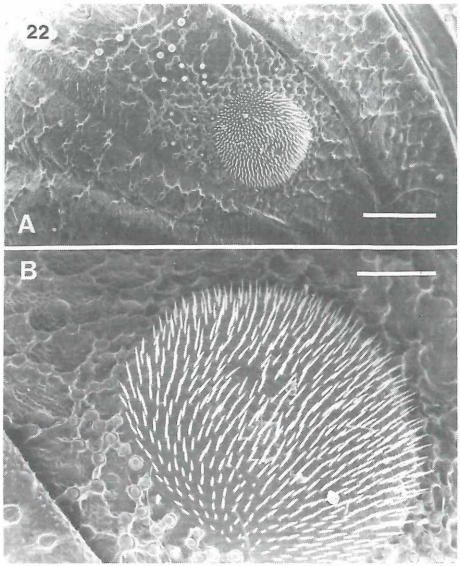

Fig. 22: Lateral organ of A8. **A:** overview with network of cuticular ribs and surrounding group of PCOs. Scale: 250 μm. **B:** Close-up showing short stiff bristles. Scale 100 μm.

lower amplitude, and distinct croaking pulses with higher amplitude and carrier frequency. These latter calls only occurred after tactile disturbance of the pupa and increased in number and amplitude after heavy molestation. The rustling component was not audible to the unaided human ear and could only be perceived using the stethoscope. The croaking calls, in contrast, were easily audible when the pupae were hold in the hollow hand, or when they were placed on the table with the stethoscope held above them (without direct contact to its membrane). Accordingly, the rustling component is entirely substrate-borne, whereas the croaking calls contain at least some air-borne portion.

Only one observation was made with respect to pupal myrmecophily. A pupa was caged with a single *Crematogaster* worker (this ant had already been associated with the caterpillar for 10 d), but during the following 7 d the ant only occasionally antennated the pupa. The spiracles with their PCO clusters were most attractive. The ant survived well until the the end of the experiment without access to any additional food.

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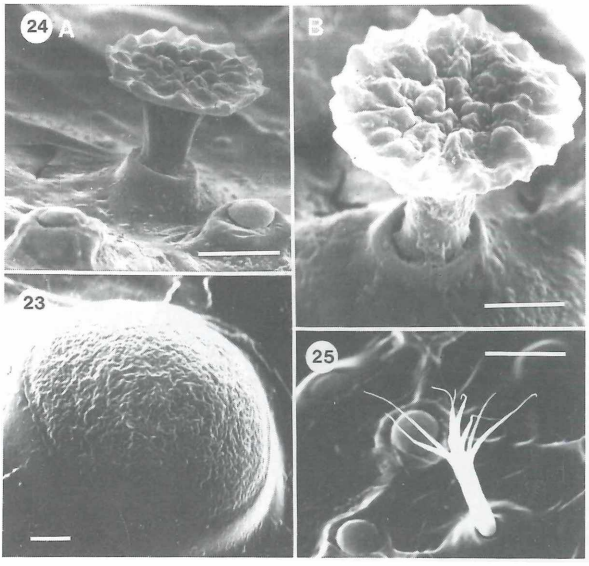

Figs. 23–25: Pupal setae. **Fig. 23:** Pore cupola organ with wrinkled sieve-plate. Scale: 5 μm. **Fig. 24:** Trumpet seta. **A:** lateral view, note the typical socket and PCOs. Scale: 15 μm. **B:** Close-up of distal end with folded surface. Scale: 10 μm. **Fig. 25:** Dendritic seta from the PCO field of A6 spiracle. Scale: 25 μm.

Preimaginal mortality and parasitism

Two fourth instar larvae (one found with ants in attendance, the other without ants) died in captivity after 10 and 12 d, respectively. The causes of death remain unclear (probably an infectious disease). All other L_3–L_5 caterpillars developed well with the exception of 1 L_3.

This caterpillar was collected on 19 November with 3 workers of *Rhoptromyrmex wroughtonii* in attendance. The larva fed well in captivity and was constantly visited by 1–3 of these ants. After 7 d, however, a parasitoid larva (possibly Ichneumonidae?) emerged from the ventral side. The parasitoid span a small silk web to which it attached itself (Fig. 8). In addition, it had secreted a foamy white substance (source unknown), and one worker ant was constantly biting into this protective barrier consisting of silk and secretion. The two remaining ants still intensively antennated the larva and were attracted to its DNO and PCOs. The TOs remained functional (Fig. 19) and were everted, whenever the caterpillar was disturbed (e. g. touching with forceps). The 3 ants were fixed on the day of parasitoid emergence.

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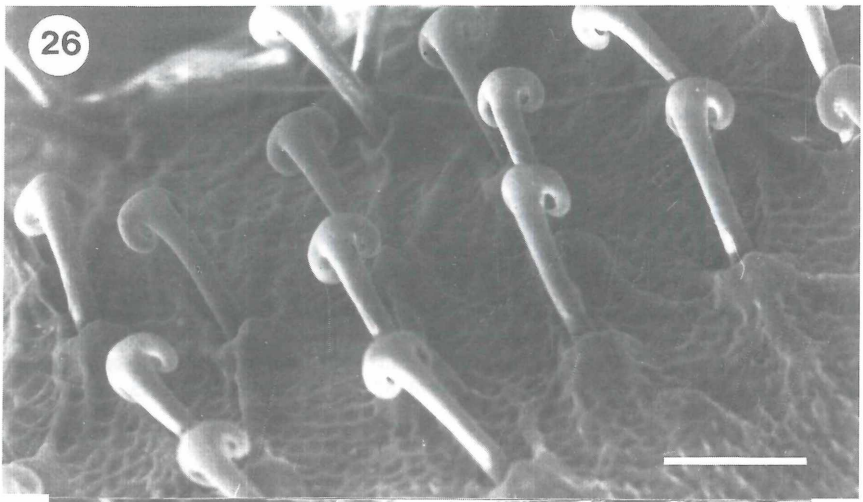
During the following 6 d, the parasitoid fed externally from the ventral side, with its head and thorax bored into the host's body. Unfortunately, the parasitoid then died prior to pupation. The *S. florimel* larva was, however, still able to produce the typical 2-component vibrations until 7 d after the parasitoid's emergence. At the eighth day, the larva became mute and was fixed.

No other cases of parasitism were observed, even though several larvae had been collected without an ant-guard.



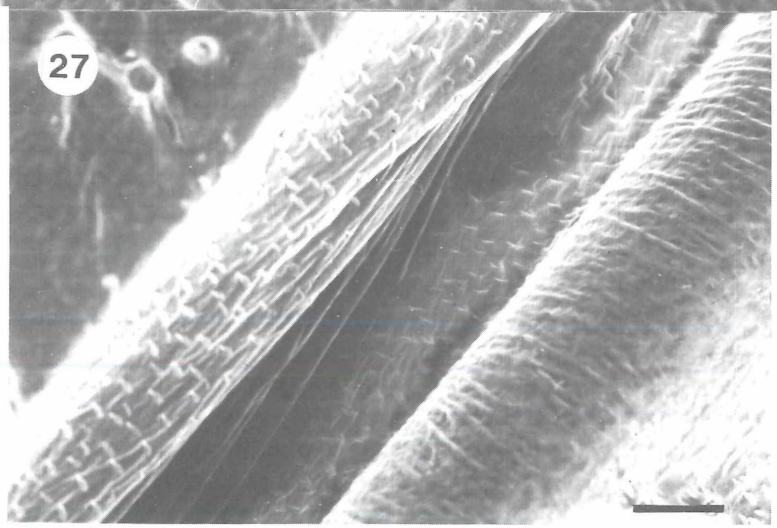


Fig. 26: Cremastral hooks. Scale: 50 μm. **Fig. 27:** Stridulatory organ between A5 and A6. Scale 50 μm.

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Discussion

Comparative morphology and systematic aspects

The caterpillar of *Surendra florimel* is very similar in habitus to that of *S. vivarna* (Horsfield [1829]) as well as to the larva of *Amblopala avidiena* (Hewitson 1877) (Maschwitz et al. 1985, Uchida 1985). All *Surendra* species known thus far as larvae (*quercetorum, vivarna, florimel*) as well as *A. avidiena* feed on hostplants of the family Mimosaceae with finely pinnate leaves (e. g. *Albizzia, Acacia*), upon which their shape and colour pattern provides a perfect camouflage. The pupa of *A. avidiena* is stout as in *Surendra* (Uchida 1985). The similarities between the early stages of *Surendra* species with *Amblopala avidiena* in external habitus and hostplant choice suggest a closer affinity of these two genera (also Eliot, pers. comm.). Probably, *Amblopala* should be transferred into the *Surendra* section of the Arhopaliti, instead of being placed in an *Amblopala* section of the Thecliti (Eliot 1973). This view is further supported by the deviating hostplant relationships of all true Thecliti hairstreaks. Thecliti larvae almost exclusively feed on Fagaceae and related families, but never on legumes (Shirozu 1962, Fiedler 1991 a).

Among the Arhopaliti, rough descriptions of larvae and pupae are available for only a few species (*Arhopala, Flos, Thaduka*). All these have very flat, onisciform caterpillars with a full set of myrmecophilous organs (Bell 1915, Common & Waterhouse 1981, Maschwitz et al. 1984). Detailed descriptions of their epidermal organs, however, do not exist. Ballmer & Pratt (1989) only note the presence of prothoracic "sensory" (= filiform) setae in *Arhopala pseudocentaurus* (Doubleday 1847) [erroneously given as *centaurus* (Fabricius 1775)] and *Flos areste* (Hewitson 1862).

Hence, I have examined one mature larva of *Arhopala amphimuta* (Felder & Felder 1869), using a stereo microscope (magnification × 70). This very flat, myrmecophilous caterpillar (Maschwitz et al. 1984) has a well developed DNO and a pair of inconspicuous TOs which are not inserted in elevated bulges. On the prothoracic shield there is one pair of filiform setae, and the whole body is literally covered with short mushroom-like setae very similar to those of *S. florimel.* Amidst these there are numerous longer setae with a roughly sculpturized, distally broadened hair shaft (probably corresponding to the curved type 5 setae of *S. florimel*). True dendritic setae appear to be absent (possibly their detection requires SEM techniques), while the spiracles

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and the bases of the TOs are surrounded by longer straight bristles. PCOs occur scatteredly all over the larva, but their number and density is low except at the DNO. Like in *S. florimel*, the membraneous DNO area carries a very dense cluster of PCOs.

Unfortunately, I have not yet seen a pupa of any *Arhopala*. Available pupal descriptions lack usable details concerning setal equipment. VIEHMEYER, in a little known paper (1910), described what he believed to be functional pupal DNOs in Indian *Arhopala amantes* (HEWITSON 1862) and in another undetermined *Arhopala* species from the Philippines. Judging from a photograph given by COMMON & WATERHOUSE (1981), the pupa of the Australian *A. centaurus* has a similar organ. The pupae of these species are all tended by ants and may be found in ant nests, but these interactions (including secretion acts) have never been reported in sufficient detail. In *S. florimel* pupae the DNO is clearly not functional. Other *Arhopala* species also lack a functional DNO. For example, MASCHWITZ et al. (1984) did not explicitly note ant-associations in *A. amphimuta* and *A. moolaiana* (MOORE [1879]). Accordingly, a functional DNO is most likely an apomorphic trait of only one sub-group (or several sub-groups?) of *Arhopala* (species with a pupal DNO belong to the informal groups g and h of *Arhopala* sensu BRIDGES 1988). It is yet impossible to state whether trumpet setae universally occur among the pupae of Arhopaliti.

As it stands, the morphology and distribution of secondary setae are quite similar in *S. florimel* and *A. amphimuta* larvae. This is in accordance with the supposedly rather close relationship of these two genera. Nevertheless, the diversity of epidermal organs found within the subtribe Arhopaliti merits further comparative work based on a larger sample of species. In particular, data on the function of the various epidermal organs are required. At present, only some speculative inferences are possible. One hypothesis is that the mushroom-like setae are probably involved in some way in the myrmecophilous interactions of *Surendra* and *Arhopala* caterpillars. In *S. florimel* these setae are mainly present around the myrmecophilous glands, and in *A. amphimuta* the whole body, being covered with such setae, is intensively licked by attendant *Crematogaster* ants (MASCHWITZ et al. 1984). Their surface structure (with cavities) likewise supports a glandular function. It may be noteworthy that many highly myrmecophilous Aphnaeini caterpillars possess similar hairs (CLARK & DICKSON 1971). The pupal trumpet setae could also be glandular, but their function in connection with myrmecophily (if there is any) remains obscure. A

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possible attractive role of dendritic setae in ant-associations of lycaenid immatures has already been suggested by BALLMER & PRATT (1989).

The most enigmatic epidermal structures found in *S. florimel* are the lateral dome-shaped organs on A8. I am not aware of any description of a similar structure of lycaenid larvae or pupae. VIEHMEYER (1910) did not mention these, but explicitly noted the presence of "only . . . a pair of slight depressions in the chitin". With regard to their position, the pupal dome-shaped organs could be homologous to the larval TOs, but at present there are neither histological nor behavioural data confirming this idea. In captivity, *Crematogaster* ants did not pay special attention to these organs. Further Arhopaliti pupae should be surveyed for the presence and structure of the dome-shaped lateral organs.

Few data exist on the detailed morphology of larvae or pupae from the subtribe Thecliti which is thought to be closely related to Arhopaliti (ELIOT 1973). BALLMER & PRATT (1989) noted that "sensory" (= filiform) setae are present in *Hypaurotis crysalus* (EDWARDS 1873) and *Habrodais grunus* (BOISDUVAL 1852) larvae, whereas dendritic setae are stated to be absent in the latter (both species from North America). Larvae of *Neozephyrus ("Quercusia") quercus* (LINNAEUS 1758) have dendritic setae only on A8 (possibly rudiments of former TOs?; cf. KITCHING & LUKE 1985). Pupae of the same species possess numerous trumpet setae quite similar to those of *Surendra florimel* pupae on the whole dorsal and lateral surface except the wing cases (FIEDLER, unpubl.). In addition, there are several dendritic setae on either side of the prothoracic tergite. Mature larvae of *Thecla betulae* (LINNAEUS 1758) possess dendritic setae on the prothoracic shield and around the spiracles of A7 and A8 (investigated at magnification × 70; FIEDLER, unpubl.). One pair of filiform setae exists on the prothoracic plate. Besides, both *N. quercus* and *Th. betulae* larvae are mostly covered with rather long straight bristles (as typical for myrmecoxenous species) and possess PCOs, but lack a DNO and TOs (for possible rudimentary structures see KITCHING & LUKE 1985).

These scattered findings are difficult to evaluate with respect to the phylogenetic relationship between Thecliti and Arhopaliti. The presence of pupal trumpet setae in both subtribes could represent a synapomorphy, but this hypothesis has to be tested comparing a broader range of species. Strikingly, trumpet setae have hitherto been recorded only from pupae of true coppers (Lycaenini: WRIGHT 1983, FIEDLER 1988).

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Whether the trumpet hairs of Arhopaliti, Thecliti and Lycaenini constitute a synapomorphy derived from a common ancestor, is highly doubtful. Nevertheless, since the origin of the Lycaenini is still enigmatic, the Theclini should not a priori be excluded as a possible sister-group (but see SCOTT & WRIGHT 1990).

Among the remaining Theclini subtribes Ogyriti and Zesiiti, available information on the morphology of immatures is so scarce (Zesiiti: KITCHING 1983) that any phylogenetic discussion has to be deferred.

Ecology and behaviour

Surendra florimel is a true forest species that does not colonize large open habitats. The larvae are food specialists with a strong preference for very young growth of their mimosaceous hostplants. In addition, at least younger instars have been observed to visit EFNs for long periods. This behaviour has been reported for some myrmecophilous riodinids, e. g. *Thisbe irenea* (STOLL [1780]), *Synargis mycone* (HEWITSON 1865) and one *Nymphidium* species (DEVRIES & BAKER 1989, DEVRIES 1991 a), as well as for a few lycaenids. *Jalmenus evagoras* (DONOVAN 1805) caterpillars, for example, drink EFN secretions and occasionally even honeydew released by homopterans sharing the same hostplants (PIERCE 1983). ATSATT (1981) and PIERCE (1983) have suggested that myrmecophilous Riodinidae and Lycaenidae preferably use hostplants bearing EFNs, and recently DEVRIES (1991) provided support to this hypothesis using data on New World Riodinidae. *S. florimel* well matches this trend.

Eggs and larvae of *S. florimel* were always found singly. This can only be explained by the choosy oviposition behaviour of the females, since larval cannibalism was never observed (even in a small container with almost 10 larvae). It remains unknown whether the eggs evaporate a deterrent pheromone (like in certain Pieridae: DEMPSTER 1992). In *S. vivarna*, MASCHWITZ et al. (1985) found eggs singly or in small groups (up to 3) on tender plant tissues, suggesting a similar oviposition behaviour. Although ants frequently visit the EFNs of young hostplant shoots, they seem to play no role as additional oviposition cue, because eggs as well as young larvae were sometimes found in the absence of ants. The only egg-laying act that I have observed directly, likewise occurred on a shoot with no ant actually tending the EFN. Laying eggs singly without using ants as cues is typical for facultative myrmecophiles (PIERCE & ELGAR 1985). Interestingly, these authors

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have included *S. quercetorum* in their listing of lycaenids that probably do use ants as oviposition cue, based on BELL's old records (1915). In the light of the observations presented here on related species, this assignment seems somewhat unlikely. LARSEN (1987), however, has reported from South India that adults of *S. quercetorum* assemble on *Acacia* shoots infested with ants. In this species also the butterflies, in company with ants, appear to drink EFN secretions. This might indicate a more intricate relationship towards ants and hostplants. The adult food resources of *S. florimel* remain unknown.

S. florimel larvae maintain a close, but unspecific and facultative symbiosis with ants. Six ant species from 5 genera in 3 subfamilies were observed in the field, and in experiments with *Polyrhachis bellicosa* permanent symbiotic associations likewise occurred. Thus, further ant taxa can almost certainly be found as tending partners. PIERCE (1987) has proposed the hypothesis that obligatory ant-associations are more common in the tropics. In contrast, FIEDLER (1991 a) has sampled evidence that the majority of tropical lycaenids are facultative myrmecophiles. The observations on *S. florimel* support this latter view, but clearly the question is still open, since the early stages of the vast majority of Arhopaliti hairstreaks remain unknown.

One caterpillar observed in an *Oecophylla smaragdina* territory was untended, which could suggest that the larvae of *S. florimel* are rather unattractive to these ants. I have, on one occasion, observed the same with *Jamides celeno* (CRAMER [1775]): one mature larva feeding on a young shoot of *Saraca thaipingensis* (Caesalpiniaceae) was consistently ignored by *Oecophylla* workers, whereas on the same tree numerous caterpillars of the obligate myrmecophile *Anthene emolus* (GODART [1824]) were constantly visited by these ants.

The benefits *S. florimel* larvae might derive from myrmecophily remain to be explored. The observed level of parasitism was low, the only parasite having emerged from a tended larva. The ants, on the other hand, permanently harvested secretions, and their longevity in captivity indicates that larval secretions of *S. florimel* may represent a substantial supplementary nourishment.

In contrast to most previous records of ant-reactions towards TO eversions (FIEDLER & MASCHWITZ 1988, FIEDLER 1991 a), *S. florimel* caterpillars are able to alert a rather broad taxonomic range of tending ants with the help of these organs. The mechanism of alerting ants via the TOs is still speculative (alarm pheromone mimics?, cf. HENNING 1983).

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The biological meaning of the substrate-borne vibrations produced by Lycaenidae immatures remains a matter of speculation. Based on experimental work with one riodinid and a comparative study of many riodinids and lycaenids, DEVRIES (1991 b) has claimed that "calling" only occurs among myrmecophilous species and increases the attractiveness of larvae or pupae to ants. In contrast to this assumption, myrmecoxenous species are known to call (SCHURIAN & FIEDLER 1991, FIEDLER 1992). *S. florimel* avidly produces vibratory signals that consist of two components in larvae and pupae. Two vibratory components are also widespread among other Lycaenidae caterpillars (DEVRIES 1991 b) as well as pupae (DOWNEY & ALLYN 1978). In the case of *S. florimel*, the permanent rustling ground component might possibly help to attract ants, whereas the croaking pulses with higher amplitude were only observed upon disturbance, suggesting a defensive rather than communicative function. Permanent vibrations of *Arhopala* larvae have also been noted by earlier authors (*A. pseudocentaurus:* NORMAN 1949; *A. centaurus:* VALENTINE 1984).

In lycaenid pupae the "pulse component" is often audible to the human ear and thus contains air-borne elements. In the larvae of a few lycaenid species, the "pulse component" has been occasionally perceived as audible (*Thereus pedusa* (HEWITSON [1867]), *Jalmenus evagoras, Hypochrysops apollo* MISKIN 1891: PIERCE 1983, DEVRIES 1991 b). On one occasion I also heard clicking pulses of a *S. florimel* larva sitting on the stethoscope membrane. It remains to be tested whether an air-borne component in certain larval signals does occur regularly, indicating the presence of true stridulation also in caterpillars, or whether it is a mere resonance artefact. Most calls of lycaenid larvae are entirely substrate-borne and probably pruduced via rhythmic pulses of high-frequency muscle contractions (DEVRIES 1991 b, FIEDLER & KIRCHNER, unpubl.).

Colour plate, Figs. 1–8:
Fig. 1: *Surendra florimel* female, ventral side. **Fig. 2:** Mature (fifth) instar caterpillar. **Fig. 3:** Mature caterpillar prior to pupation. Note colour change into reddish brown. **Fig. 4:** A worker of the ant species *Polyrhachis bellicosa* harvesting a secretion droplet from the DNO of a mature caterpillar. **Fig. 5:** Second instar larva sitting with the head at an extrafloral nectary. **Fig. 6:** Freshly moulted fourth instar larva tended by *Technomyrmex albipes.* Arrow: cast skin of previous instar. **Fig. 7:** Pupa, dorsal view. **Fig. 8:** Caterpillar with emerged parasitoid larva attached to a silk web.

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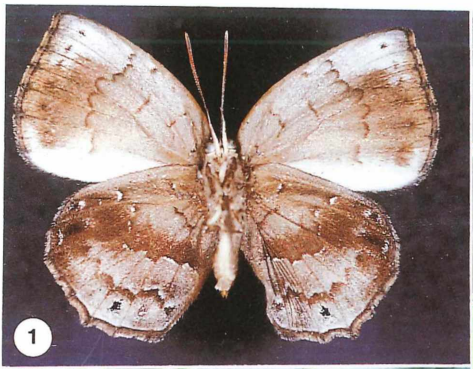

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Remarkably, the parasitized *S. florimel* larva retained its vibratory abilities for days even after the parasitoid's emergence. I have observed the same phenomenon with caterpillars of *Callophrys rubi* (LINNAEUS 1758), *Glaucopsyche alexis* (PODA 1761) and *Jamides* sp., but only in larvae parasitized by braconid wasps (FIEDLER, unpubl.). In contrast, lycaenid caterpillars that were parasitized by tachinid flies lost their vibratory abilities 1–3 d prior to the emergence of the tachinid maggots (e. g. *Thecla betulae, Callophrys rubi, Jamides* sp.; FIEDLER, unpubl.). Thus, the loss of vibratory abilities in parasitized lycaenid caterpillars depends on the specific extent of the internal tissue damage due to the parasitoids' differential feeding habits. It is unknown whether the parasitoids gain some protective benefits if their hosts remain able to vibrate. This might be true in the case of *S. florimel,* since the parasitized larva also remained attractive for its attendant ants.

PIERCE (1983) has already noted that carcasses of parasitized lycaenid larvae may remain attractive for ants up to 10 d. In *S. florimel,* even the TOs remained functional, but this is not a universal trait. While in one *Jamides* caterpillar parasitized by a braconid wasp the TOs remained active after the parasitoid's emergence, other lycaenids parasitized by braconids or tachinid flies lost the ability to evert their TOs. Several *Jamides* larvae parasitized by tachinid flies (*Aplomyia* near *flavisquama*) were left by their attendant ants even 1–2 d prior to the parasitoids' emergence (FIEDLER, unpubl.). The behavioural and ecological interactions between myrmecophilous lycaenid immatures, their ant-guard and parasitoids clearly constitute a rewarding field for future research (also NASH 1989).

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ENTOMOLOGISCHE NOTIZ

Zur Ökologie von *Thyris maculata* HARRIS 1839 (Lepidoptera, Thyrididae)

Die Gattung *Thyris* ist mit wenigen Arten holarktisch verbreitet und wurde von THIELE (1986, "Die Gattung *Thyris* HOFFMANNSEGG, 1803", Atalanta **17:** 105–146) monographisch bearbeitet. In den USA fliegen 2 Arten, *T. maculata* HARRIS 1839 (= *perspicua* WALKER 1856) und *T. sepulchralis* GUERIN 1832; beide bevorzugt im östlichen Nordamerika in gemäßigten Klimazonen. Wenn auch die beiden Arten in Amerika einigermaßen bekannt sind, so soll die Gelegenheit doch benutzt werden, ihre Ökologie in Amerika zu Vergleichszwecken mit der europäischen Art zu diskutieren. THIELE (1990, "Dritte Ergänzung zum Beitrag über 'Die Gattung *Thyris* HFFMSGG.' (Lep., Thyridae [sic!])", Atalanta **21:** 283–288) berichtete über das Flugbiotop am Potomac River in Maryland und die Zucht, konnte aber keine Futterpflanzen im Biotop nachweisen.

Die Ökologie von *T. maculata* konnte in den Sommern 1990 und 1991 von mir eingehend studiert werden. Die Art fliegt in der Umgebung von State College (Zentral-Pennsylvania) weit verbreitet in allen Feuchtbiotopen und in Bachauen, stets eng mit ihrer Futterpflanze *Clematis virginiana* L. (Ranunculaceae) verbunden. *T. maculata* wirkt schon auf den ersten Blick wie ein "Doppelgänger" der europäischen *Thyris fenestrella*, ist aber noch kleiner und bunter.

Die Art kommt von Ende Mai bis Ende Juli lokal, aber stellenweise häufig vor. Offensichtlich ist sie polyvoltin mit mindestens 2, möglicherweise auch 3 Generationen, wobei die einzelnen Generationen fließend ineinander übergehen. Die Tiere fliegen genau wie *T. fenestrella* nur in der näheren Umgebung der Futterpflanze und bevorzugen hellen Sonnenschein. Als Nektarquelle wird eine breite Vielfalt von Pflanzen angenommen; besonders häufig werden die zur Flugzeit blühenden *Erigeron philadelphicus* und *Erigeron annuus* (Asteraceae)